THE INTERNAL ANATOMY OF THE MYDAS FLY.*

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INTRODUCTION.

The following work is a report on the internal anatomy of the Mydas fly, *Mydas clavatus* Drury. In a survey of the literature dealing with certain insect groups it was found that nothing is known concerning the internal anatomy of the primitive flies of the Family *Mydaidæ*. Indeed, very little information of any kind is found which discloses the habits or life history of this large Dipteron. It was thought that a knowledge of the internal anatomy might indirectly reveal some of the life habits. A few carefully killed and fixed specimens of *Mydas clavatus* being available, a detailed dissection and microscopical examination was made. The Mydas flies are not common in Ohio, only two species have been reported from the state. The species used is a large, dusky, brown fly in which the dorsal sclerite of the second abdominal segment is marked by an orange band, and the antennæ are clavate and black. It is occasionally taken along Lake Erie on the sandy beach at Cedar Point, where the specimens used in this study were collected. Usually individuals of the group are found on dry, decaying logs or tree stumps. Owing to the scarcity of material it was necessary to use the same specimens for gross dissection and for the microscopical examination, consequently extreme care was taken during all manipulations.

I wish to express my thanks to Dr. C. H. Kennedy under whose supervision this investigation was carried on and also to Prof. J. S. Hine for the identification of specimens.

METHODS.

Only three specimens were available, two females and a male. These flies were killed and fixed in Kahle's Fixative and then preserved in 70% alcohol.

Gross Dissection. It was slightly unwieldy to work with the legs and wings attached therefore these were first clipped from

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the body. The insect was then pinned out in a dissecting pan and covered with alcohol. All dissections were made under 70% alcohol with the aid of the binocular microscope. The alcohol was frequently renewed in order to insure preservation during gross dissection. The entire dorsal body wall was first carefully removed in minute particles after which the muscles of the thorax were taken out, exposing the alimentary canal for study. The nervous system and the reproductive systems were studied after the alimentary canal had been removed. No histological work was attempted with these systems, but drawings of the gross structures were made free hand while using the binocular microscope.

Microscopical Technique. The parts of the alimentary canal were cut into convenient lengths, run through the alcohols, cleared and imbedded in paraffin. All sections were cut seven microns thick and stained with a double stain of Delafield's haemotoxylin and eosin. The drawings were made with the aid of a camera lucida.

The Anatomy of the Digestive System.

The alimentary canal is a comparatively short tube and suggests the carnivorous habit. In the higher Diptera the digestive system may reach a length almost twice that of the insect itself, and appears as a convoluted mass filling the abdomen. In the Mydas fly, however, it extends as a straight tube throughout its length with the exception of several convolutions in the hind gut where it loops back upon itself twice. Plate I, Figure II.

In insects the fore gut is an invagination of the ectoderm at the anterior end and is called the stomodaeum. The hind gut is formed in a similar fashion and is a posterior ectodermal invagination called the proctodaeum. Connecting these two regions is the mid gut which is derived from endodermal tissue. In correlation with the external epithelium the epithelial lining of the fore and hind guts secretes chitin which is found lining these regions as a definite membrane. The parts of the alimentary canal will be discussed in the following order:

A. Mouthparts.
B. Fore Gut.
   1. Pharynx.
   2. Oesophagus.
   3. Oesophageal Valve.
   4. Salivary Bulb.
   5. Salivary Duct.
   6. Salivary Glands.
   7. Crop.
C. Mid Gut.
   1. Gastric caeca.
   2. Stomach (proper).
   3. Pyloric Valve.
D. Hind Gut.
   1. Malpighian Tubules.
   2. Intestine.
      a. Rectum.

I. GROSS STRUCTURES.

A. Mouthparts.

The mouthparts of the Mydas fly have been worked out and figured by Peterson (1916), and present a type of structure similar to that in the robber flies and horse flies, but distinctly less specialized. This is another evidence of the predaceous method in acquiring food, although there is no record which shows that the adult Mydas fly has ever been observed actually attacking another animal.

B. Fore Gut.

The *pharynx* is the anterior end of the alimentary canal and lies just posterior to the mouth. Food is conveyed by means of the pharynx to the oesophagus; in this fly there is no essential difference between the structure of the pharynx and the oesophagus.

The *oesophagus* begins posterior to the pharynx and extends to the anterior end of the mid gut. Its diameter gradually increases in size until the posterior end is twice as large as the anterior. The oesophagus gives the appearance of an opaque, chalky white tube.

The *crop* is a dilatation of the ventral wall of the oesophagus. This is an out-pocketing which is so pronounced in the Mydas fly that the crop itself lies in the abdomen and is connected with the oesophagus by means of a long slender tube. The tube lies just beneath the stomach, branching off at the posterior end of the oesophagus and continuing until it reaches the second abdominal segment. The crop functions as a food reservoir.

The *oesophageal valve* represents the posterior limit of the fore intestine and is really a prolongation of the fore gut into the mid gut.

The *salivary glands*.—"The salivary duct extends through the hypopharynx to its distal end." (Peterson). Here the tube enlarges to form the salivary bulb, then narrows again and eventually passes upward and back through the head and neck. Before it leaves the head it divides forming two ducts which extend through the neck to the thorax and lie, one on either side of the oesophagus close to the anterior end of the thoracic cavity as thickened convoluted tubes. These posterior thickenings are the glands proper. Secretions pass from the glands to the ducts and are then transferred to the hypopharynx. There they are mixed with the food and are probably the first agents in digestion.

C. Mid Gut (Stomach).

The *gastric caeca* are two pouches which represent out-pocketings in the anterior end of the *stomach* and lie at right angles to the remainder of the alimentary canal. They occupy the entire anterior end of the thoracic cavity. Numerous projections on the surface of the caeca appear as evaginations which increase the secreting surface. Similar secreting sacs are also found posterior to the caeca but not as extensively, and they do not occur on the posterior half of the stomach. The stomach extends to the pyloric valve. It has a uniform diameter for two-thirds of its length and then gradually increases in size.

The *pyloric valve* is the posterior limit of the mid gut. It is the point of insertion of the malpighian tubules.

D. Hind Gut (Intestine).

The *malpighian tubules* define the anterior limit of the hind gut. There are four tubes, two branching from the dorsal surface and two branching from the ventral surface. These twine in and out among the digestive organs and other body structures. They are excretory in function, extracting urinary wastes from the body.

The *intestine* includes all the structures of the hind gut. The ileum is the smaller anterior end of the hind gut and the colon the larger posterior part. In the Mydas fly there is no distinguishable difference in the size or structure of these regions.

The *rectum* represents an abrupt enlargement of the posterior end of the hind gut. The surface of the rectum is spotted with the bases of rectal glands or papillæ which project into the rectal lumen. These are confined to three general rows and are about thirty-three in number. No definite function is known for these glands.

II. HISTOLOGICAL STRUCTURES.

A. Fore Gut.

The following tissues can be demonstrated in a histological examination: (1) a chitinous intima, (2) epidermal layer, (3) longitudinal muscle layer, (4) circular muscle layer. The innermost layer is an *intima of chitin* which is secreted by the epidermal cells. It is a non-cellular membrane, and forms a thick layer of very flexible chitin. The next layer is composed of flattened *epithelial cells*. In most places it was possible to distinguish cell walls quite easily but in others the entire layer resembled a syncytium. Immediately outside the epithelium is a layer of *longitudinal muscle fibers*. These are arranged in the form of a dense network several fibers in thickness. The outermost layer of the oesophagus is composed of *circular muscle fibers* which occur in scattered bundles. See Figures I and II, Plate II.

The *salivary glands* are part of the fore gut and are therefore ectodermal in origin. They are composed of a single layer of columnar cells which contain large nuclei. There is an intima of chitin present which lines these glands. Figure IV, Plate II shows the salivary gland as it appears in cross-section.

The *oesophageal valve* is the division between the fore and mid gut and is formed by an invagination of the fore gut into the mid gut. Several kinds of epithelial cells are found in the valve making it impossible to determine just which cells are derived from the fore gut and which from the mid gut. In the oesophagus are found the flattened epithelial cells described above. At the entrance to the valve the form of the cells changes abruptly and a disc composed of columnar epithelium is formed. Immediately posterior to the disc the cells decrease in size and number and their long axis becomes parallel to the position of the digestive tract. The tube is very narrow here. Figure I, Plate II shows this narrow passage filled with chitin and the tips of underlying cells which have extended inward so that they almost close the lumen. At the posterior margin of the valve the epithelial cells are considerably elongated and very numerous. These cells form a heavy collar which makes a thick wall at the anterior end of the stomach.

The ring of cells at the anterior and the collar of cells at the posterior end give the valve the appearance of an ambidisc. The region between the two discs is heavily supplied with circular muscles, which possess the ability to shut off the passage to the stomach and thus afford an opportunity for food to pass to the crop. The epithelial cells in the mid gut just posterior to the oesophageal valve are thicker and not as long as those found in the posterior disc. Their inner surfaces are covered by a peritrophic membrane which arises at the anterior end of the mid gut and appears as though it were secreted by the cells of the digestive epithelium.

The tube leading to the *crop* begins immediately anterior to the first disc of cells in the valve. This tube is lined with an intima of chitin, then a layer of squat epithelial cells. The outside is provided with a heavy layer of circular muscles.

In Figure I, Plate II the oesophageal valve and the tube leading to the crop are shown in longitudinal section.

B. Mid Gut.

A histological examination of the mid gut reveals the following tissues: (1) peritrophic membrane, (2) enteric epithelium, (3) circular muscle layer, (4) longitudinal muscle layer. The mid gut shows a non-specialized type of structure which is common to lower insects generally. The *peritrophic membrane* appears to be secreted by the gastric epithelium. It appears as a distinct non-cellular membrane which functions as a protection to the epithelium. It covers the cells and shows up very distinctly in cross section. Figure III, Plate II shows how closely the membrane lies to the epithelial layer. The next layer is that of the actively functioning endodermal *epithelial cells*. There is no specialized type of nidi or cell nests. The cells which are destroyed in holocrine secretion are replaced by others which are narrow, elongate cells at the bases of the active, secreting cells, and are interspersed among them. They are not confined to any definite region but occur singly, scattered among the functioning cells. The digestive epithelium is composed of columnar cells which are grouped together forming projections into the lumen of the alimentary canal. The cells are narrow at their bases and flare at their tips, due perhaps to the crowded condition of the developing cells. The flaring outer ends of the cells form irregular projecting folds. At the very apex of these cells are numerous granules which resemble the basal bodies of cilia, and form a distinct line around the outer edge of the cells when viewed in cross section.

Between the cells of the digestive layer and the muscles layer is an area filled with numerous branching filaments which stain red with eosin. The finger-like extensions of this layer are projected between the cells of the epithelium. The branched condition and the extension of the filaments between the cells has led the writer to believe that they are tracheoles whose tips are found among the cells.

The bundles of *circular muscle* lie outside the above layer and form a closely united ring around the stomach wall. The *longitudinal muscle* fibers are found in groups just outside the circular layer. The muscles are not closely united and form loose bundles usually consisting of three or five fibers.

C. Hind Gut.

The tissues of the hind gut are arranged in the following manner: (1) an inner intima of chitin, (2) an epithelial layer, (3) a circular muscle layer, (4) a longitudinal muscle layer and (5) around the malpighian tubule there is a peritoneal membrane.

The *plyoric valve* represents the boundary between the mid and hind guts. The epithelial cells of the mid gut are greatly elongated and their tips are directed posteriorly, projecting, as a ring into the cavity of the hind gut. The malpighian tubules are inserted between the mid and hind guts. At their origin the tubules are formed of slender, elongate cells which are crowded very closely together. These cells do not possess the striated border common to the cells in the malpighian tubule. The cells gradually increase in size going away from the basal end of the tubule, and contain larger nuclei. Figure III, Plate III shows a longitudinal section through the pyloric valve.

In the region behind the pyloric valve and just anterior to the rectum is an area in which the intima forms a thin layer that appears as a heavy line around the inner edges of the epithelial cells. The latter, as found in this region of the intestine, are almost square in shape, and appear like columnar cells. The muscle layers are not highly developed.

In the *malpighian tubules* the epithelial cells are very large, and their inner ends are lined with a striated border which appears as if composed of cilia. At the bases of the striations granules are found which show up very distinctly. Whether or not these are true cilia is unknown. Figures I and II, Plate III show sections through the malpighian tubules.

In the *rectum* the intima of chitin is not as thick as that in the fore gut but is considerably thicker than the same layer elsewhere in the intestine. It extends as a wavy membrane over the epithelial cells. Figure V, Plate III shows the arrangement of the tissue in the rectum. The epithelium is composed of flattened cells much like those in the fore gut. The circular muscle layer is developed to a high degree. The bundles appear to be piled up in heaps, giving the inside a folded appearance. The longitudinal muscle layer contains larger fibers than have been encountered anywhere else in the gut.

The *rectal papillæ* project finger-like into the lumen of the intestine. There are approximately thirty-three papillæ whose external openings dot the surface of the organ, and are confined to three general rows. In the higher Diptera the number of papillæ is much smaller. Each papilla is composed of large epithelial cells which probably are pushed inward due to the proliferation of cells from an active, growing region at the tip. The cells here are smaller than at the base of the papilla, where large irregular cells occur. The cells are arranged in a double row, each row a single cell in thickness. Between these two rows of cells numerous tracheoles are found. There is a smooth layer of chitin around the papilla without spines or other structures common to more specialized forms of papillæ. The rectal papilla of the Mydas fly shows this structure in its primitive form.

THE NERVOUS SYSTEM.

I. Brain.
  a. Protocerebrum.
    Protocerebral lobes.
    Optic lobes.
  b. Deutocerebrum.
    Antennal Nerves.
  c. Tritocerebrum.
  d. Suboesophageal ganglion.

II. Ventral Nerve Cord.
  a. Ganglia.
  b. Lateral Nerves.

A superficial examination of the nervous system of the Mydas fly reveals the following external structures. The brain or cephalic ganglia lie in a fused mass in the head. A double row of united ganglia lies on the ventral floor of the thoracic and abdominal cavities.

The most obvious structure and one which includes the greatest part of the brain is called the *protocerebrum*. It is composed of two distinct parts, the protocerebral lobes and the optic lobes. The protocerebral lobes are fused along the median line and form a bilobed mass, which indicates its original derivation from a pair of ganglia in the optic segment. This nerve mass enervates the compound eyes and the ocelli. At the junction of the protocerebral lobes three nerves are given off. Two of these unite at their distal ends to form the saddle shaped structure observed in side view in Figure VIII, Plate I. This structure is pigmented on its outer border over the area that lies beneath the external ocelli. The third nerve enlarges at its distal end to form a bulb-like organ which is also pigmented on its outer surface and lies just beneath the median ocellus. The optic stalk is continuous with the protocerebrum and enlarges to form the huge optic lobes. These lobes form most of the brain and are developed to the same extent as the compound eye.

The deutocerebrum lies a little anterior and ventral to the protocerebrum. The antennal nerves are given off from this portion of the brain.

The third part of the brain or the tritocerebrum lies posterior and ventral to the deutocerebrum and is composed of two united lobes. The mouthparts are enervated from nerves which arise from this part of the brain and in the *sub-oesophageal ganglion* which is indistinguishable from the tritocerebrum.

The nerve cord lies in a double row of united ganglia along the ventral wall of the thorax and abdomen. Only two pairs of ganglia are found in the thorax showing that there is a concentration of ganglia in this region. From these ganglia nerves are given off which supply the wings and legs. From the ganglia in the abdomen pairs of lateral nerves arise. There is some fusion of ganglia in the posterior of the abdomen since three pairs of nerves arise here instead of the usual one pair. Centralization of ganglia has progressed to some extent in both the thorax and abdomen but not appreciably.

The outstanding features of the nervous system in the Mydas fly are the marked development of the optic lobes and the cephalization in the thoracic and abdominal ganglia. This condition shows the first stages in cephalization which has proceeded to such a marked degree in the muscid flies.

THE MALE REPRODUCTIVE ORGANS.

I. Testes.
II. Vas deferens.
III. Ejaculatory sac.
IV. Ejaculatory duct.

The *testes* are considerably smaller than the ovaries. A pair of them lies in the third abdominal segment, ventral to and on each side of the alimentary canal. The testes are spherical bodies which have a diameter slightly greater than the vas deferens.

The *vas deferens* consists of a pair of tubes which extend from the testes to the posterior. They are white and coil several times before they finally unite to form a single tube. In the posterior of the abdomen these tubes have formed such a convoluted mass that in the specimen used it was impossible to determine the exact place at which the tubes united. In Figure V, Plate I the dotted lines indicate the joining of the two tubes to form one as it might occur. After the tubes of the vas deferens have joined the diameter of the resulting tube remains the same as that of the other tubes until it reaches its posterior end. Here it narrows gradually and finally merges with the ejaculatory duct. The latter begins immediately back of the entrance to the ejaculatory sac.

The *ejaculatory sac* is a blind, pouch-like tube which branches to the right of the vas deferens. Its diameter is the same as that of the vas deferens where it branches off. Gradually, however, the tube enlarges and forms a large sac.

The *ejaculatory duct.*—The remainder of the system posterior to the branching of the ejaculatory sac is called the ejaculatory duct. It has a very large diameter as it nears its end.

THE FEMALE REPRODUCTIVE ORGANS.

I. Ovaries.
  a. Ovarioles.
II. Oviducts.
III. Vagina.
IV. Seminal receptacles.
V. Colleteria.

The female Mydas fly in which the reproductive organs were observed had apparently been fertilized and engaged in egg laying. The abdomen was distended by the numerous eggs which filled the body cavity. Some of these were already equipped with chitinous shells. Figure IV, Plate I shows a drawing made while the eggs were still in place in the abdomen.

Ovaries.—The ovaries are composed of numerous sac-like structures called ovarioles. These are joined at their bases to form a duct which eventually unites with one of the oviducts. It was impossible to trace the connections between the ovarioles in this specimen. The ovarioles and their contents completely filled the abdomen and were firmly pressed together, distorting some of the other organs. The *ovarioles* are tubes in which the eggs are formed. Each ovariole appears to end freely in the body cavity without any attachment to the body wall or other internal structure. The eggs lie as chains in an ovariole, one behind the other. The oldest eggs lie nearest the union with the oviduct. An ovariole consists of several distinct parts. The distal end is termed the terminal filament. A thin peritoneal layer covers the outside of an

ovariole and is continuous with the oviduct. Within this lie the developing ova. The type of egg here found clearly shows that *Mydas clavatus* does not deposit fully formed larvæ but the egg must undergo a period of incubation after it is laid.

The *oviducts* are thin walled tubes which lead from the ovaries to the vagina. They extend posteriorly and form the vagina after they unite.

The *vagina* extends from the union of the oviducts to the outside.

There are three *seminal receptacles* which enter the vagina at the point where it opens to the outside. Each receptacle is a blind, pouch-like tube which has an inner chitinous lining. This is visible through the external layers and gives a faint yellow tinge to the tubes at their tips. As the eggs pass through the vagina sperms are transferred from the seminal receptacles and enter the eggs through the micropyle.

The *colleteria* are two long white tubes which enter the vagina just posterior to the seminal receptacles. Figure III, Plate I shows these pushed back out of the abdominal cavity. They lie at either side of the vagina in the normal fly. These glands are functional in that they produce a sticky substance. The substance produced in the Mydas fly probably serves to attach the eggs to some object when oviposited.

The *egg* is one millimeter in diameter. At the end which lies toward the anterior of the mother is a faint white spot which shows up distinctly against the brown color of the egg. This is called the micropyle.

SUMMARY.

The Mydas fly is a representative of one of the primitive families of Diptera. A study of the internal anatomy confirms the evidence derived from the external anatomy and other sources in regard to their relative systematic position.

The alimentary canal is a generalized food tube which shows no particular specialization in any direction. The length of the tract and the structure of the mouthparts indicates that the fly is carnivorous in its food habits.

The concentration of ganglia has not proceeded to any great degree, while centralization of the whole system is greatly like that of lower Diptera.

The chorion of the egg is composed of a hard chitinous material and precludes the idea that the female is able to deposit mature larvæ. This characteristic of the eggs as found in the abdomen of the female necessitates a longer or shorter period of incubation after the egg has been deposited.

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EXPLANATION OF PLATES.

PLATE I.

Fig. I. A dorsal view of the nervous system showing the position of the brain, ganglia, and the main nerves which branch from the ventral nerve trunk.
Fig. II. A dorsal view of the alimentary canal.
Fig. III. A dorsal view of the female reproductive system, which shows all parts of the system except the ovaries.
Fig. IV. The abdomen of the female Mydas fly showing the arrangement of the eggs.
Fig. V. The male reproductive system shown in a dorsal view.
Fig. VI. Side view of the brain of the Mydas fly with the optic lobes removed.
Fig. VII. Dorsal view of the brain as it lies in the head.
Fig. VIII. Dorsal view of the brain after it has been tipped forward in order to show the sub-oesophageal ganglion.

PLATE II.

Fig. I. Longitudinal section through the oesophageal valve, oesophagus, gastric caeca, and the tube leading to the crop.
Fig. II. A view of part of the oesophagus taken from a cross-section.
Fig. III. Part of the cross-section through the mid-gut, which shows the arrangement of the epithelium into papillæ-like projections.
Fig. IV. Cross-section of a salivary gland.

PLATE III.

Fig. 1. Cross-section of a malpighian tubule.
Fig. II. Longitudinal section of a malpighian tubule.
Fig. III. Longitudinal section through the pyloric valve showing the insertion of a malpighian tubule.
Fig. IV. Cross-section through the hind gut.
Fig. V. Longitudinal section of the rectum which is cut through a rectal papilla.

ABBREVIATIONS.

Ant. Nerv.	Antennal Nerves.	Per. Memb.	Peritrophic Membrane.
Circ. Mus.	Circular Muscle.	Perit. Memb.	Peritoneal Membrane.
Col.	Colleteria.	Rec.	Rectum.
Ej. Duct.	Ejaculatory Duct.	Sal. Bulb.	Salivary Bulb.
Ej. Sac.	Ejaculatory Sac.	Sal. D.	Salivary Duct.
Epith.	Epithelium.	Sal. Gl.	Salivary Gland.
Gast. Caec.	Gastric Caecæ.	Sp. Rec.	Sperm Receptacle.
Int.	Intestine.	Stom.	Stomach.
Long. Mus.	Longitudinal Muscle.	Trach.	Tracheoles.
Malp. Tub.	Malpighian Tubule.	Ts.	Testes.
Oes.	Oesophagus.	Vag.	Vagina.
Opt. Lobe.	Optic Lobe.	Vas. Def.	Vas Deferens.
Ovid.	Oviduct.	Vent. Nerv. Cord.	Ventral Nerve Cord.

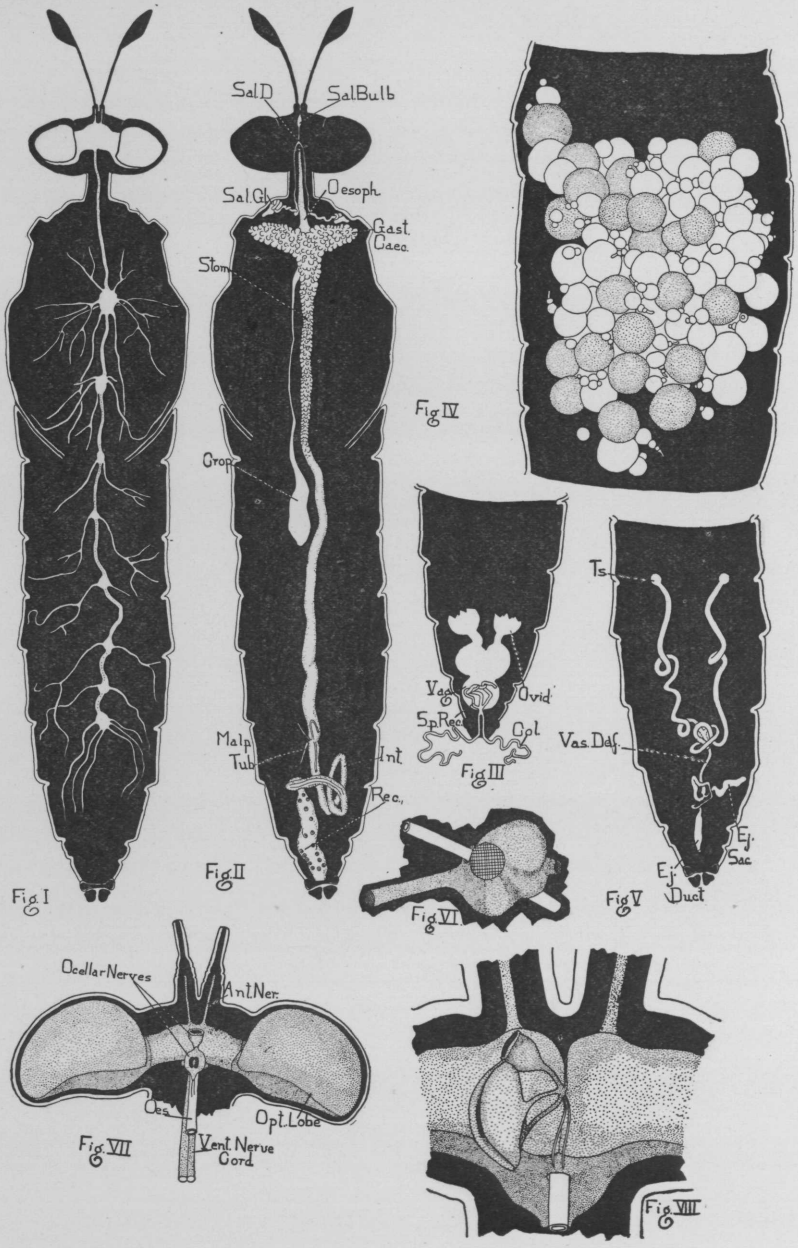
Sal.D
Sal.Bulb
Sal.Gl.
Oesoph.
Gast.
Caec.
Stom.
Crop.
Malp.
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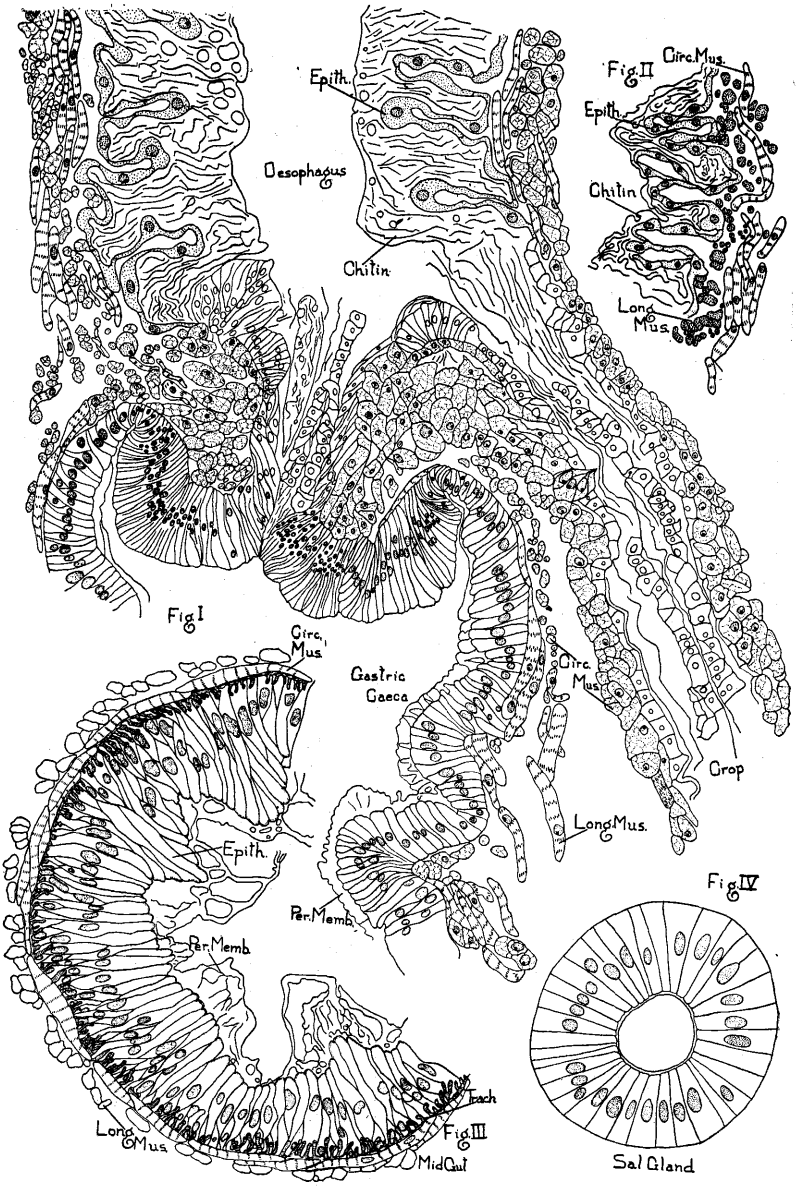
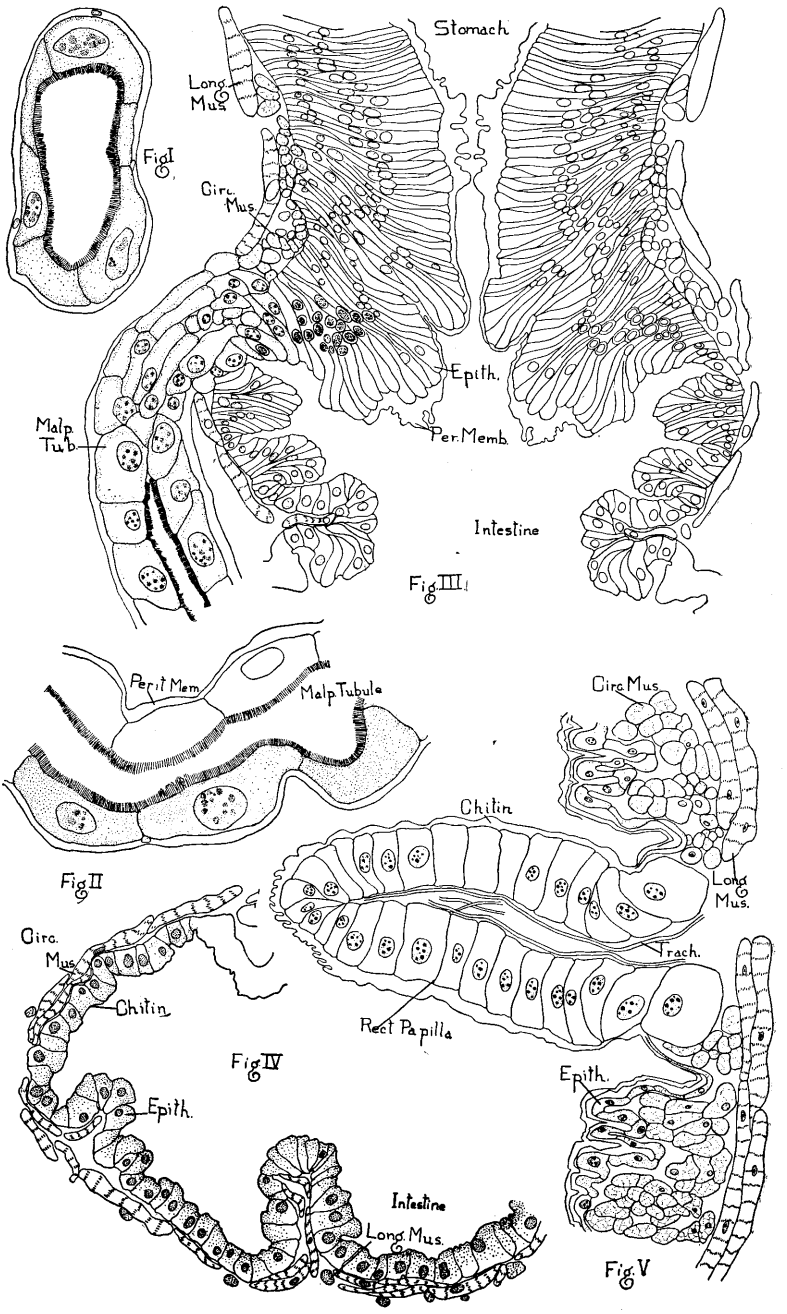
Fig I
Fig II
Fig IV
Vag.
Ovid.
Sp.Rec.
Gol.
Fig III
Ts.
Vas.Def.
Ej.
Sac.
Ej.
Duct
Fig V
Fig VI
Ocellar Nerves
Ant.Ner.
Oes.
Opt.Lobe
Vent.Nerve
Cord.
Fig VII
Fig VIII


Epith.
Oesophagus
Chitin
Fig I
Circ. Mus.
Gastric Caeca
Circ. Mus.
Crop
Long. Mus.
Epith.
Per. Memb.
Per. Memb.
Long. Mus.
Trach.
Fig III
Mid Gut
Fig II
Circ. Mus.
Epith.
Chitin
Long. Mus.
Fig IV
Sal Gland


Stomach
Long Mus
Fig I
Circ. Mus
Epith.
Per. Memb.
Malp Tub
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Circ Mus
Chitin
Long Mus.
Trach.
Circ. Mus.
Chitin
Rect Papilla
Fig IV
Epith.
Epith.
Intestine
Long Mus.
Fig V